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Title: What to copy: the key factor of observational learning in striped jack (*Pseudocaranx dentex*) juveniles

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14 Abstract

15 Animals in social environments can enhance their learning efficiency by observing
16 the behaviour of others. Our previous study showed that learning efficiency of
17 schooling fish increased through observation of the behaviour of trained
18 demonstrator conspecifics. The present study aimed to verify the key factor of
19 observational learning by investigating what information is important for social
20 transmission of feeding information. A striped jack *(Pseudocaranx dentex)* observer
21 was provided with one of five observation treatments: (a) pellets observation,
22 where pellets were dropped near the aeration in an adjacent tank; (b) responding
23 conspecific observation, where a trained conspecific demonstrator responded to the
24 aeration without food in the adjacent tank; (c) foraging conspecific observation,
25 where a conspecific demonstrator foraged near the aeration in the adjacent tank;
26 (d) nearby pellets observation, where pellets were dropped in a transparent column
27 near the aeration in the observer tank, and (e) foraging heterospecific observation,
28 where a filefish (*Stephanolepis cirrhifer*) demonstrator foraged near the aeration in
29 the adjacent tank. The response to the aeration in these observers was compared
30 with that of controls who did not observe any behaviour. Only individuals which
31 observed foraging conspecifics showed a response to the aeration after observing.
32 These results suggest that observer fish acquire feeding information not through
33 recognition of prey items or through imitation of the demonstrator, but through the
34 vicarious reinforcement of a conspecific for foraging.

35

36 Keywords: behavioural transmission, conditioning, copying, fish cognition, social
37 learning

Introduction

Learning in a social environment can potentially be facilitated by social learning (Kleiman and Eisenberg 1973). In social learning, an individual acquires behaviour and information through observations of and interactions with other individuals. This style of learning has the potential to enhance an individual's adaptation to the living environment. For example, prey location can be learned through observations of associating shoal mates in feeding sites, without the energetic expenditure of food searching, e.g., in Atlantic salmon *Salmo salar* (Brown et al. 2003). The anti-predator behaviour of the Japanese flounder (*Paralichtys olivaceus*) can also be enhanced through observation of conspecifics, without the risk of predation (Arai et al. 2007).

About half of the teleost fishes in the world live socially in a school for at least part of their lives (Shaw 1978) and thus have the opportunity to acquire information through social learning. Indeed, some studies have found that fish acquire survival skills by social learning in various life history contexts, such as predator avoidance (Brown and Laland 2001; Kelly et al. 2003), orientation behaviour (Warner, 1988; Fukumori et al. 2010), feeding (Reader et al. 2003; Schuster et al. 2006; Webster and Laland 2008), and mate choice (Witte and Nobel 2011).

Social learning mechanisms have been studied in a number of species, including rats (Zohar and Terkel 1991), dogs (Miller et al. 2009), primates (Hopper et al. 2008; Tennie et al. 2010), and birds (Klein and Zentall 2003; McGregor et al. 2006). For example, McGregor et al. (2006) found in pigeons (*Columba livia*) that, even when demonstrators were not rewarded while being observed, observers of pecking behaviour made pecking responses more frequently than did observers of stepping behaviour. This study provided evidence of imitation simply as a process

in which 'B learns some aspect(s) of the intrinsic form of an act from A' (emphasis original; Hopper 2010). Hopper (2010) also defined 'ghost display' conditioning, where an observer is able to reach a predetermined goal from seeing only the pertinent parts of a given task/apparatus without an active model operating it.

While many researchers have investigated the function of observational learning in fish (i.e. what fishes learn through observation), there are few studies regarding the mechanisms of observational learning (i.e. how fish learn their behaviours through observational learning). Recent studies have shown that their cognitive capacity in many domains is comparable with that of non-human primates (Brown et al. 2011). For example, fishes have evolved complex cultural traditions (Brown and Laland 2011; Bshary et al. 2002), that is, they not only recognize one another, but they can also monitor the social prestige of and dominance relations amongst others (Griffiths 2003; Grosenick et al. 2007). Thus, they may be equipped with mechanisms for the observational learning that are similar to those of animals of higher orders.

Our previous study confirmed the ability for observational learning in jack mackerel (*Trachurus japonicus*) juveniles: fish that observed other individuals feeding at the aeration in an adjacent tank were conditioned to aeration as a stimulus to initiate feeding more quickly than fish that did not observe this conspecific behaviour (Takahashi et al. 2012a). Here we tried to tease apart the process of observational learning and thus elucidate the essential mechanism of this social behaviour. We proposed their observational learning could be explained by one of the following hypothetical processes: (i) fish are conditioned to aeration with the presence of food through watching the foods and aeration stimulus, which could be confirmed by a 'ghost display condition'; (ii) observer fish copy demonstrator fish in their response to aeration, suggesting that they are capable of

imitation; or (iii) observer fish acquire feeding information by observing demonstrator fish foraging near the aeration, indicating that they need a full demonstration. By testing these conditions separately, this study investigated how observational learning is formed in conditioned feeding with the aeration stimulus.

We used striped jack (*Pseudocaranx dentex*) in this study. They consistently form a school when they attain the juvenile stage at around 20 mm standard length (SL; Masuda and Tsukamoto 1998) and therefore have many opportunities to acquire information from conspecifics, much like *T. japonicus*. This species is more resistant to stress from isolation than *T. japonicus* (Takahashi, personal observation). Furthermore, in this study, we used a heterospecific demonstrator observation treatment to investigate the possibility of observational learning between species. Using a demonstrator fish that has a different shape from that of the observer, the treatment confirmed the importance of the appearance of a model for observational learning. Filefish (*Stephanolepis cirrhifer*) were used as the heterospecific demonstrators. ALthough they live in sympatry and share feeding resources with *P. dentex* (Masuda, personal observation), the body form is distinctly flat compared with that of *P. dentex*, which is more spindle-shaped.

Materials and methods

Fish

Hatchery-reared *P. dentex* were purchased from Yamasaki Giken Co., Ltd. or Pacific Trading Co., Ltd. and were transported to the Maizuru Fisheries Research Station, Kyoto University. About a hundred juveniles were kept in each of two 500 l transparent polyethylene tanks supplied with filtered seawater at a rate of 4 l per min and with strong aeration (600 ml / min). Rearing tanks were indoors, and water temperature was kept at about 25°C using a heater and thermostat. The fish

were fed with commercial pellets (Otohime C2 and Otohime S2, Marubeni Nisshin Feed Co., Ltd.) to satiation once or twice a day until the fish were to be used for the experiment. All the fish were kept in a tank for at least one month to be weaned on pellets, as all were confirmed to forage actively on pellets near the water surface. SL of all to fish used was measured after the experiments. Fish mean SL was 76.2 mm (standard deviation = 1.2 mm), and there was no difference between treatments (according to an analysis of variance: $F_{5, 44} = 1.65$, $P > 0.05$; Table. 1). Juveniles used for the experiment ranged in age from 90 to 120 days old. It was not possible to identify sex in these juveniles.

Apparatus and Procedure

Transparent glass tanks (length × width × height: 60 × 30 × 35 cm) were set up in a temperature-controlled room and covered with black vinyl sheets except for one side. Seawater was continuously added to the experimental tanks and drained using a siphon to maintain a depth of 20 cm. Tanks were separated by a black sheet to reduce disturbance from experimenters. A video camera (HDR-CX550, Sony Co., Tokyo, Japan) above the experimental tank allowed recording of the fish behaviour during the experiment.

An air stone was positioned set at the centre of each tank, and aeration was remotely controlled and was turned off except in the conditioning trial, when aeration was set to be gently turned on to provide approximately 12 ml of air per minute. The tanks of the observer fish and the demonstrator fish were arranged so that the uncovered sides of its tanks faced each other, and a removable black board (length × height: 60 × 35 cm) was placed between tanks except during an observation trial.

A single fish was introduced into the demonstrator tank, and that fish was

used as a demonstrator. All demonstrator fish were conditioned to respond to aeration as a conditioned stimulus and feeding pellets as an unconditioned stimulus, as in Takahashi et al. (2012b); that is, 30 s after the onset of aeration, pellets were dropped near the aeration. The demonstrators were trained until they showed a prominent response to aeration without pellets. Different demonstrator fish were used for each observer fish, except for the foraging heterospecific observer. Some of the observer fish that had been trained to respond to aeration were used as demonstrators after the test trial, but no demonstrator fish were used as observers.

Single fish were randomly selected from each rearing tank, introduced into one of four replicate observer tanks on the previous day, and allowed to acclimate overnight. A few pellets were provided before initiating the experiment, which began once the observer fish ate these initial pellets. When the fish was foraging for the pellets, the black board between the tanks was removed at 30 min before the start of observation trials so that demonstrator fish were visible to observer fish in the adjacent tank. Observer and demonstrator fish used for an experiment trial were drawn from the same stock tank. Therefore, they were likely to be familiar with each other during the observation trial.

Observation trial

Observer fish were provided with one of the following treatments, performed by demonstrator fish in the adjacent tanks: pellets, responding conspecific, foraging conspecific, nearby pellets, and foraging heterospecific observation (Fig. 1a-e). Five observation trials were provided for each observer, and the observation trial was video recorded to evaluate fish behaviour. The response to aeration of these treatment groups was compared with that of the control group, where no

demonstrator fish was provided (Fig. 1f). Eight fish were used in the control group and in each observational treatment except for the nearby pellets treatment, in which five fish were used.

In the pellets treatment, pellets were dropped near the aeration in a demonstrator tank that contained no demonstrator fish. The observation trial lasted for 60 s; after aerating for 30 s, three to five pellets were dropped near the aeration source three times at 15 s intervals. In the responding conspecific treatment, an observer fish was allowed to observe a *P. dentex* demonstrator that was responding to aeration without pellets. The observational trials ran for 30 s, which was the same as the duration of aeration in the demonstrator tank. In the foraging conspecific observation treatment, the observer fish observed the behaviour of a conspecific demonstrator that was responding to aeration and foraging pellets near it. The observation trials ran for 60 s; after the aeration was turned on for 30 s, three to five pellets were dropped near the aeration three times at 15 s intervals.

The nearby pellets treatment investigated the possibility of observational learning in a situation where the observer can recognize the food at close range within the observer tank, because there was a possibility that during the pellets treatment, observer fish would not be able to recognize the pellets in the adjacent demonstrator tank. In this treatment, the pellets were so that the observer could see them but the fish was not allowed to forage the pellets. A transparent oval column (10cm × 7.5cm × 30 cm height) was positioned at the centre of the conditioning tank, and the air stone was put outside of the column. An observer was provided with the observation trial for 60 s, during which the aeration was turned on for 30 s, and after that the pellets were dropped into the oval column near the aeration three times at 15 s intervals. The pellets were removed using a

194 pipette after turning off the aeration.

195 To conduct heterospecific observation trials, two *S. cirrhifer* (93 mm and 95
196 mm SL) were captured using a cage trap in Maizuru Bay (35° 49' N; 135° 36' E) and
197 transported in a bucket of seawater. They were kept in a 500 l transparent
198 polyethylene tank, like that was to the *P. dentex*. Rearing tanks were indoors, and
199 water temperature was kept at about 25°C using a heater and thermostat. After
200 confirming active foraging on pellets (Otohime S2) in the water column, they were
201 transferred to two separate tanks. They were trained until both showed prominent
202 responses to aeration, and could thus be used as demonstrators. Five observation
203 trials were conducted in the same manner as the foraging conspecific observer
204 treatment, i.e., after the onset of aeration for 30 s, pellets were dropped near
205 aeration for 30 s. After the experiment, *S. cirrhifer* were measured in their SL and
206 subsequently released at the capture site.

207 Five observation trials were conducted with about 30 min intervals for each
208 of the observation treatments. After the fifth trial, the black separation board was
209 placed between observer and demonstrator tanks to avoid further interaction
210 between them; in the nearby pellets treatment, the column was removed from the
211 observer tank. Each observer fish was given a test trial at 30 min after the fifth
212 observation trial.

213

214 Test trial

215 A test trial was conducted to confirm the observer fish's response to aeration in
216 observation tank without feeding pellets; aeration was turned on for 1 min. The
217 response was then compared with that of the control group. In the test trial,
218 behaviour of each observer and control was video recorded for 2 min, 1 min pre-
219 aeration and 1 min post-aeration.

220

221 Behavioural analyses

222 Attraction to the demonstrator tank was used as an index of the observation
223 behaviour in the first observation trials except for the nearby pellets treatment.
224 The attraction was measured by the staying duration of fish within 7.5 cm (approx.
225 one fish SL, and 25% of experimental tank) from the side of the demonstrator tank.
226 Attraction behaviour was measured for 30 s in each observation trial: while pellets
227 were dropped near the aeration three times in the pellets treatment, while the
228 aeration of the demonstrator tank was turned on (i.e. demonstrator fish responded
229 to aeration without pellets) in the responding conspecific treatment, and while
230 pellets were dropped near the aeration three times (demonstrator fish foraged near
231 aeration) in the foraging conspecific or heterospecific treatment. The attraction
232 duration to a demonstrator tank was compared among observation treatments
233 using a Kruskal-Wallis test followed by a Steel-Dwass multiple comparison as a
234 post hoc test. The attraction duration to a demonstrator tank in the first
235 observation trial was also compared with 7.5 s as the significance level (chance
236 level: 25% of 30 s), in each observation treatment using a one-sample Wilcoxon test
237 (n = 8), because the data were not normally distributed.

238 In the nearby pellets observation treatment, attraction behaviour to pellets
239 was measured using the duration of fish staying near the aeration (within 7.5 cm
240 around the oval column). The duration was measured to 30 s in each of the pre-
241 aeration and post-aeration periods, and then the average durations of the five
242 observation trials (n = 5) were compared between pre- and post-aeration periods
243 using a paired *t*-test to confirm observers' recognition of the pellets. The data
244 showed normal distribution and homogeneity of variance between pre- and post-
245 aeration.

In the test trials, observers' frequency of staying near the aeration in the test fish tank was used as an index of their response to aeration. The staying frequency in the aeration area (which was defined as 20 × 20 cm surrounding the aeration stone) was counted during 2 s every 1 min of the pre-aeration and post-aeration periods. Attraction to the aeration was evaluated by the staying index, calculated by subtracting the frequency during pre-aeration from that during post-aeration. To investigate how well the observation trials promoted transmission of response to aeration, the staying index of each observation treatment was compared using a Kruskal-Wallis test, and each observation treatment was compared with the control treatment using Steel's multiple comparison. Some of the data lacked homogeneity of variance between treatments; this is why the analyses were conducted using non-parametric methods.

Results

There was a significant difference in the attraction to the demonstrator tank among treatments in the observation trials (Kruskal-Wallis test: $n = 8$, $\chi^2_{3, 32} = 11.2$, $P < 0.05$); the attraction duration in the responding and foraging conspecific treatments was significantly longer than that in the pellets observer treatment (Steel-Dwass multiple comparison test: pellets vs. responding conspecific: $n = 8$, $t = -2.76$, $P < 0.05$, pellets vs. foraging conspecific: $n = 8$, $t = 2.97$, $P < 0.05$; Fig. 2). Furthermore, the attraction behaviour to the demonstrator tank in the responding and foraging conspecific observer treatments significantly differed from the chance level, but that was not the case in pellets observers or in foraging heterospecific observers (one-sample Wilcoxon test; pellets: $n = 8$, $t = 6$, $P > 0.05$, responding conspecific: $n = 8$, $t = 2$, $P < 0.05$, foraging conspecific: $n = 8$, $t = 1$, $P < 0.05$, foraging heterospecific: $n = 8$, $t = 17$, $P > 0.05$; Fig. 2). In the nearby pellets

observation treatment, the attraction duration near aeration increased from pre- to post-feeding (paired t-test; df = 4, t = -2.64, P < 0.05), suggesting that the observer fish were attracted by pellets in the oval column during the observation trial.

In the test trials, there was a significant difference in staying index between treatments (Kruskal-Wallis test; $\chi^2_{4,\ 37}$ = 11.5, P < 0.05); the staying index in the test trial in the foraging conspecific treatment was significantly different from the control treatment (Steel-Dwass multiple comparison test; foraging conspecific: n = 8, t = -2.46, P < 0.05; Fig. 3). However, there was no such difference in staying index between other treatments and the control (pellets: n = 8, t = -0.11, responding conspecific: n = 8, t = -0.00, nearby pellets: n = 5, t = -0.54, foraging heterospecific observer: n = 8, t = -0.50; P > 0.05).

Discussion

Naïve observer fish that were given the opportunity to see a conspecific model were more likely to attend to the adjacent 'demonstration' tank, regardless of whether model fish was eating food pellets (foraging conspecific treatment) or not (responding conspecific treatment). However, only after seeing a conspecific eating food pellets near the aeration bubbles (foraging conspecific treatment) did the observing fish spend more time foraging by the aeration bubbles, a reaction indicative of observational learning. Merely seeing either food pellets (pellets treatment) or a responding conspecific (responding conspecific treatment) near the bubbles was not sufficient to encourage directed foraging by the observing fish. Furthermore, seeing the 'complete' demonstration of a fish eating food pellets only induced social learning when the demonstrating fish was a conspecific (*P. dentex*), not when the model was heterospecific (*S. cirrhifer*).

Whereas the *P. dentex* juveniles can learn feeding information through the

observation of foraging conspecifics, observational learning did not occur in responding conspecific observers even though observer fish watched the demonstrator responding to aeration. These results imply that the observational learning in this species was not imitation—that is, copying the responses of other individuals. Fiorito and Scotto (1992) found that octopuses (*Octopus vulgaris*) chose the 'right' ball through the observation of demonstrators, despite the fact that the demonstrator received neither reward nor punishment in the observation trial. In Laland and Williams (1997), when untrained guppies (*Poecilia reticulate*) were given the experience of swimming with conspecific demonstrators trained to take one of two equivalent routes to food, subjects preferred to use the route of their demonstrator when tested alone. These behavioural transmissions were considered imitations, a reflex response that was programmed to copy the demonstrator's behaviour. On the other hand, the formation of observational learning in this study suggested that *P. dentex* juveniles learned through recognizing a feeding conspecific near the aeration.

Fish in the pellets observation treatment were not attracted to the pellets in the adjacent demonstrator tank, so it is possible that the observer did not notice the presence of the pellets during the observation trial in this treatment. This finding also supports the idea that the presence of demonstrator fish would be important for inducing the attention of an observer. However, in the nearby pellets treatment, pellets were presented to make the observer aware of the presence of food during the observation trial, and then the observer fish was attracted to the pellets appearing near the aeration. These fish did not respond to aeration on the test trial despite the fact that they had responded to the pellets dropped near the aeration. This result suggests that ghost display conditioning was not formed in this study—thus, the observer needed the presence of a demonstrator. In other

words, the visual recognition of prey did not have any value as an unconditioned stimulus for *P. dentex* juveniles. These findings also suggest that the foraging of demonstrator fish is a substitute reward for an observer fish, which is indispensable for observational learning.

Observation of a heterospecific demonstrator did not induce observational learning in *P. dentex* juveniles. This indicates that the presence of *S. cirrhifer* did not promote the awareness of *P. dentex* in the same way as a conspecific demonstrator; the distinct appearance of *S. cirrhifer* may not trigger a cognitive response as a model for observational learning. On the other hand, Mathis et al. (1996) reported that the brook stickleback (*Culaea inconstans*) developed an avoidance response from observing the startle response of a fathead minnow (*Pimephales promelas*). The authors described that these species often form a mixed school in the natural environment and suggested that observational learning would be established within ecologically similar species, even if they are not conspecifics. Further investigations would be required to elucidate interspecies observational learning; for example, a morphologically and behaviourally similar heterospecific such as *T. japonicus* could be used as a demonstrator for *P. dentex*.

Although some past studies on social learning in fish have focused on the relation between demonstrator and observer (Duffy et al. 2009; Laland et al. 2011; Pike et al. 2010), few studies have investigated the mechanism of observational learning in fish. We would like to propose a potential mechanism of observational learning in fish in the light of the results of the present study. First, the presence of a demonstrator fish is an important factor for inducing the attention of an observer, and an appropriate demonstrator is required in this regard. Second, the foraging behaviour of the demonstrator is a fundamental factor. Our study indicated that fish cannot acquire necessary information merely with the presence

of food at the aeration or through imitating the responding behaviour to aeration of a demonstrator; instead, they learn through vicarious reinforcement from a feeding demonstrator.

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Ethical standards

All experiments were performed according to the Regulations on Animal Experimentation at Kyoto University. After the experiment, the fish were kept in the laboratory as brood stock.

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Fig. 1 Schematic drawings of observational treatments. (a) Pellets observation: pellets were dropped near the aeration in the demonstrator tank. (b) Responding conspecific observation: a trained demonstrator fish responded to the aeration in the demonstrator tank. (c) Foraging conspecific observation: a demonstrator fish fed on pellets near the aeration in the demonstrator tank. (d) Nearby pellets observation: a transparent plastic column was placed at the centre of the observer tank, and aeration was put near the column. Pellets were dropped in the column, on which the observer fish could not feed. (e) Foraging heterospecific observation: a *Stephanolepis cirrhifer* demonstrator was fed with pellets near the aeration. (f) Control: no demonstrator was provided

Fig. 2 Median attraction duration with demonstrator tank on the first observation trial of each observation treatment. Asterisks indicate the significant differences in duration from the chance level, represented by a dotted line (7.5 s: 25% of 30 s; $P < 0.05$; one-sample Wilcoxon test). Bars indicate the interquartile range (n = 8 except for nearby pellets [n = 5])

Fig. 3 Median staying index in each treatment in the test trial. Asterisk indicates that the duration significantly differed from controls ($P < 0.05$; Steel multiple comparison test). Bars indicate the interquartile range (n = 8 except for nearby pellets [n = 5])

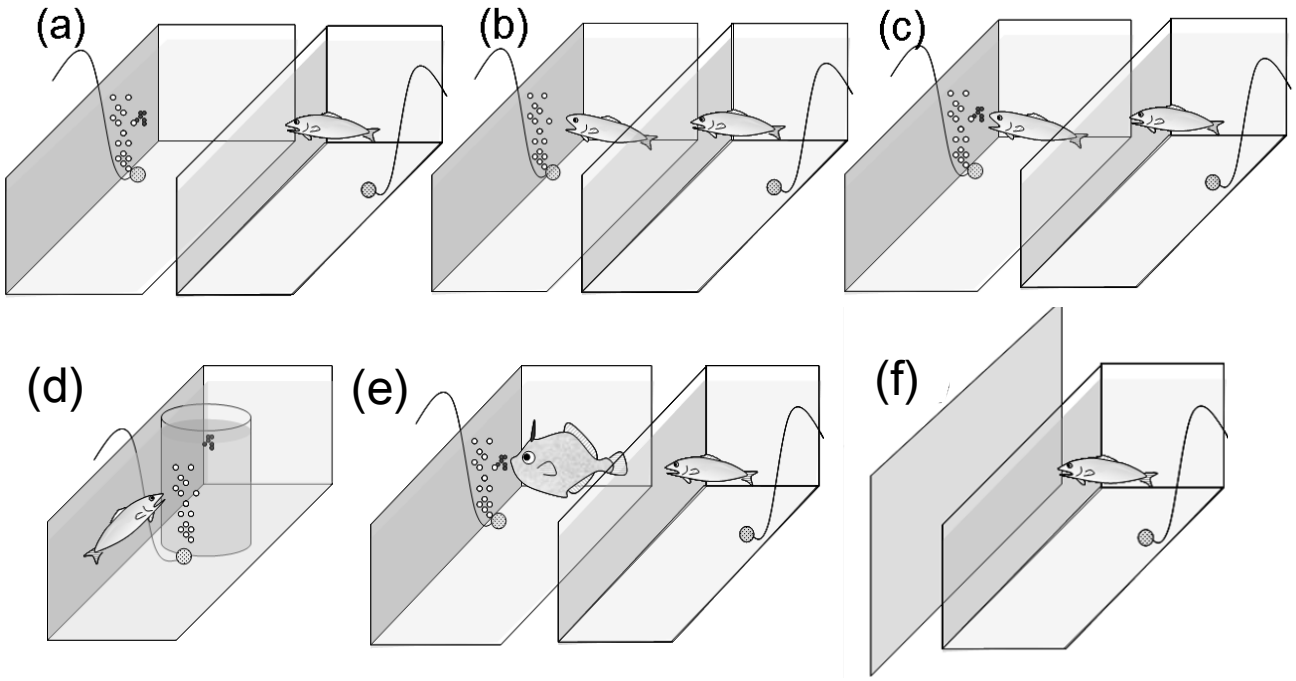
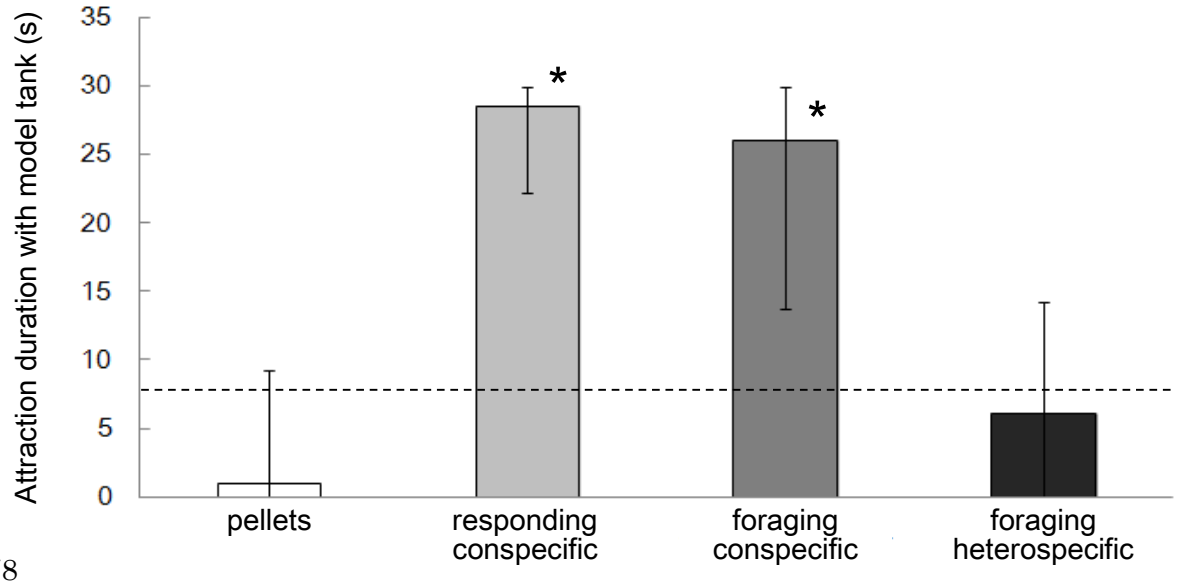


Fig. 1



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479 Fig. 2

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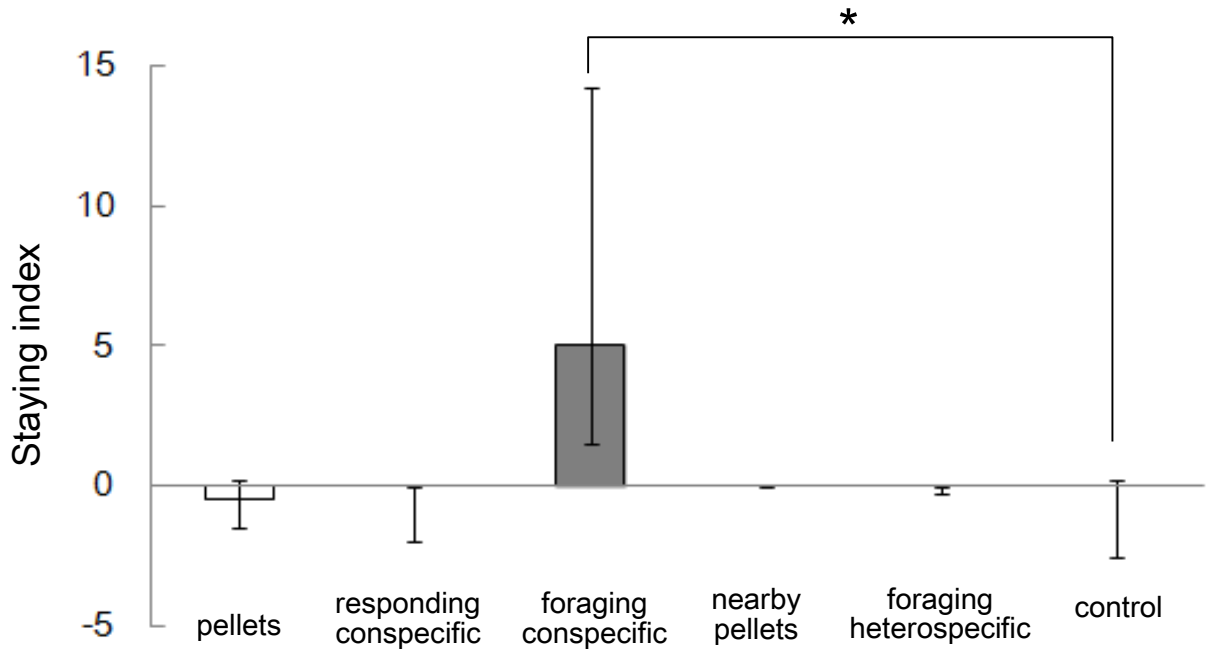

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482 Fig. 3

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